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# Reproductive Phytochemistry of Bombacaceae

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# REPRODUCTIVE PHYTOCHEMISTRY OF BOMBACACEAE: FLORAL ANTHOCYANINS AND NECTAR CONSTITUENTS

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ABSTRACT

Floral anthocyanins among Bombacaceae exhibit minimal variation and consist of three commonly occurring cyanidin glycosides. Cyanidin 3-rutinoside occurs uniquely in the genus *Pachira* among taxa surveyed. Nectars are characterized by copious volumes and being somewhat dilute and hexose rich with respect to sugars. No evidence is detectable among Bombacaceae for a nonflying-mammal floral chemistry syndrome which is distinguishable from a bat-visitation syndrome.

Key words: Bombacaceae, anthocyanins, nectar properties, nonflying mammals, amino acids.

## INTRODUCTION

The family Bombacaceae is pantropical in distribution and consists of 31 genera containing about 225 species. Representatives are often found in rain forests where they occur as canopy trees. Little is known of the ecology and less of the chemistry of Bombacaceae, except for the few species of economic interest as sources of kapok, balsa wood, and durian fruit. As is the case with other plant families occurring primarily in the tropics, there are only a limited number of species of Bombacaceae from which fresh floral material is available for study by temperate-region based botanists. The results herein are presented as an initial data base and the conclusions suggested are models against which subsequent species can be tested as they become available.

Flowers of the Bombacaceae are reported as being visited (and perhaps pollinated) by a variety of animals. As early as 1935 Porsch suggested that Bombacaceae might be pollinated by nonflying mammals (Porsch 1935). This suggestion has been confirmed by recent field observations (Janson, Terborgh, and Emmons 1981; Steiner 1981). In addition, pollination by bats has been reported for many species of Bombacaceae (Baker 1970; Heithaus, Fleming, and Opler 1975; Start and Marshall 1976; Croat 1978). Other reported flower visitors include birds and insects (Toledo 1977). Sussman and Raven (1978) suggested that bats may have replaced nonflying mammals as primary visitors to plants in several regions, including the neotropics. The present report presents some chemical characteristics of Bombacaceae flowers and their nectar which are significant for the attraction of pollinators. These floral characteristics and animal-visitor features are examined to assess the likelihood of the occurrence of distinct phytochemical syndromes for flowers visited by bats and by nonflying mammals and evidence is considered for the relictual occurrence of a nonflying-mammal syndrome among neotropical Bombacaceae.

## MATERIALS AND METHODS

Fresh flowering materials were collected for analysis from plants in cultivation at the Los Angeles State and County Arboretum, Arcadia, California; the Foster

Botanic Garden, Honolulu, Hawaii; and the Fairchild Tropical Garden, Miami, Florida.

Floral anthocyanins were purified and identified by paper chromatography using standard methods (Harborne 1967).

Nectar volumes were measured by direct pipetting and sugar concentrations were determined using a hand-held refractometer. Brix values were converted to solution-volume based values using the CRC Handbook (p. D-218, 53rd. ed.). Nectar-sugar compositions were determined quantitatively by high-performance liquid chromatography using methods reported by Freeman, Reid, Becvar, and Scogin (1984) and qualitatively by paper chromatography according to methods described by Scogin (1980*a*). Nectar amino acid concentrations were determined spectroscopically using ninhydrin as a chromogenic reagent according to the method of Yemm and Cocking (1955). Floral caloric content was calculated using the formula, calories per flower = 39 × (corrected sucrose concentration as %) × (nectar volume in ml).

Pollen counts were made by direct microscopic examination of 5-microliter aliquots of nectar. Reported values are the average of five determinations.

Nectar odor was assessed subjectively on freshly collected nectar samples by the author's nose.

## RESULTS AND DISCUSSION

### *Floral Anthocyanins*

Identified anthocyanins have been reported from only two species of Bombacaceae. Pomilio and Sproviero (1973) reported the occurrence of cyanidin 3-glucoside and cyanidin 3,5-diglucoside in the petals of *Chorisia speciosa.* Pelargonidin 5-glucoside and cyanidin 7-methyl ether 3-glucoside were reported from the petals of *Bombax malabaricum* (Niranjan and Gupta 1973). Among the taxa examined in the present study, cyanidin 3-glucoside (Cy 3-glu) was found to be universally present, frequently accompanied by cyanidin 3,5-diglucoside (Cy 3,5-diglu) (see Table 1). The only observed exception to this anthocyanin pattern was that found in *Pachira aquatica* in which cyanidin 3-rutinoside (Cy 3-rut) occurs as the second anthocyanin. The genus *Pachira* is placed in the tribe Adansonieae (Hutchinson 1967) and all three of the additional members of that tribe which were examined exhibited the commonly occurring Bombacaceae anthocyanin pair, Cy 3-glu plus Cy 3,5-diglu. No systematic significance is attached at this time to this novel (among Bombacaceae) anthocyanin combination in *Pachira,* which consists of only two recognized species (Robyns 1964). Knowledge of the anthocyanin constitution of the other species, *P. insignis,* would be of great interest in order to determine whether Cy 3-rut is a generic characteristic of *Pachira.*

Among the three putatively primitive tribes of Bombacaceae (Matisieae, Hampeae, Durioneae) (Hutchinson 1967), only a single member of the Matisieae (*Ochroma pyramidale*) was available for floral pigment study. Only cyanidin 3-glucoside occurs in this putatively primitive representative. This result is consistent with the recent hypothesis (Harborne 1977) that simple 3-glucosylation of cyanidin represents a primitive character state. By contrast, glucosylation at the 5-position and more complex glycosylation (such as the occurrence of rutinose)

Table 1. Floral anthocyanins of Bombacaceae.

| Tribe<br>Species | Major pigment(s)[1] | Minor or trace (tr) pigment (s) | Pigment source |
|---|---|---|---|
| Adanasonieae | | | |
| *Pachira aquatica* Aubl. | Cy 3-glu, Cy 3-rut | | stamen filaments |
| *Bombax malabaricum* DC. | Cy 3-glu | Cy 3,5-diglu(tr) | petals |
| *Pseudobombax ellipticum* (HBK) Dugand | Cy 3,5-diglu | Cy 3-glu | stamen filaments |
| *P. grandiflorum* (Cav.) A. Robyns | | Cy 3,5-diglu, Cy 3-glu | petals |
| Ceibeae | | | |
| *Ceiba acuminata* Rose | | Cy 3-glu | petals |
| *Chorisia speciosa* St. Hil. | Cy 3-glu, Cy 3,5-diglu | | petals |
| Matisieae | | | |
| *Ochroma pyramidale* (Cav.) Urb. | | Cy 3-glu | calyx |

[1] Cy 3-glu = Cyanidin 3-glucoside, Cy 3-rut = Cyanidin 3-rutinoside, Cy 3,5-diglu = Cyanidin 3,5-diglucoside.

at the 3-position represent derived chemical character states in the more advanced tribes.

Anthocyanin pigmentation appears to be as unsuccessful as other taxonomic characters in demarking Bombacaceae from Malvaceae. Cyanidin glucosides in general, and the 3-glucoside and 3,5-diglucoside in particular, occur commonly in Malvaceae (Timberlake and Bridle 1975). Cyanidin 3-glucoside is also the most commonly occurring anthocyanin in closely related Sterculiaceae (Scogin 1979).

The present results confirm the floral anthocyanins reported from *Chorisia speciosa* by Pomilio and Sproviero (1973), but I could not detect a pelargonidin glucoside or methylated cyanidin glucoside from *Bombax malabaricum* as reported by Niranjan and Gupta (1973).

Specialization of floral pigments (and, hence, floral colors) for the purpose of attracting different pollinator classes has been reported in other tropical families (Scogin 1980*b*). There is no evidence in support of a specialization among Bombacaceae with respect to floral pigments for pollinator class. Indeed, only minimal variation exists with respect to floral pigments among the taxa examined.

### *Nectar Properties*

*Nectar volume.*—Members of the Bombacaceae generally produce nectar in copious to extreme amounts (*Chorisia* appears to be an exception). Nectar volumes range from 0.09 ml in *Ceiba acuminata* to almost 16 ml in a single flower of *Ochroma pyramidale,* the largest nectar volume reported, to my knowledge, for a single flower. The other taxa examined produce generally 0.5–1.5 ml (exact volumes can be calculated from caloric content data in Table 2).

*Sugar concentration.*—The nectars of Bombacaceae are moderately dilute with respect to sugars, ranging from 11% to 20% as sucrose equivalents (see Table 2).

Table 2. Nectar properties of Bombacaceae.

| Species | Sugar concentration (%) | Energy content (cal/fl) | Sugar composition[1] | Amino acid concentration (m*M*) | Pollen grains per ml | Nectar odor |
|---|---|---|---|---|---|---|
| *Pachira aquatica* | 20 | 195 | Bal | 0.09 | 0 | Sweet, fruity |
| *Bombax malabaricum* | 20 | 1430 | 0.0 | 1.6 | 29,200 | Rotting fruit |
| *Pseudobombax ellipticum* | 19 | 889 | Bal | 0.39 | 2700 | Weakly fruity |
| *P. grandiflorum* | 18 | 322 | 0.350 | 0.56 | 0 | Cabbagelike |
| *Ceiba acuminata* | 17 | 66 | Hex | 0.19 | 1000 | None |
| *Ochroma pyramidale* | 13 | 7808 | 0.0 | 0.10 | 600 | Aminoid |
| *Chorisia speciosa* | No nectar detectable | | | | | |
| *Durio zibethinus* Murr. | 19 | 104 | 0.348 | 0.20 | 100 | Weakly acrid |

[1] Numerical values are (S/F + G) by weight; qualitative results are Hex = hexose rich, Bal = balanced.

All these values (especially those at the upper end of the range) are consistent with the nectar requirements of bird and mammal visitors. The average nectar sugar concentration among other bat-pollinated flowers is 19% (Scogin, unpub. data) and those plants visited by hovering and perching birds produce nectars averaging 29% and 23%, respectively (Pyke and Waser 1981). Nectar-sugar concentrations within this family thus are consistent with the frequent occurrence of visitation by mammals and birds.

*Energy content.*—The best parameter for evaluating the satisfaction of a flower visitor's energy requirements is the caloric content per flower. The caloric content of the standing nectar crop of a flower is a function of sugar concentration and nectar volume. Calculated energy content per flower for Bombacaceae is shown in Table 2. A large energy content per flower is characteristic of bird-, bat-, and nonflying mammal-visited flowers due to the large energy requirements dictated by these visitors' size and/or flight activity (Scogin 1985). Among Bombacaceae the nectar caloric content greatly exceeds the requirements of birds (Pyke 1980) and is frequently excessive even for bats, which require 10–50 kcal/day (Howell 1979; Scogin 1980*a*). The very large nectar caloric content of (at least some) Bombacaceae flowers may represent an adaptation to satisfy the energy requirements of large, nonvolant mammals and primates which visit these flowers. The body weight (mid-range) of reported Bombacaceae-visiting, nonflying mammals ranges from 95 g for *Marmosa* sp. (mouse opossum) to 5 kg for *Ateles paniscus* (spider monkey) (Nowak and Paradiso 1983). Basal energy requirements can be calculated from these weights (Altman and Dittmer 1972) and yield a range from 9 to 232 kcal/day. A typical daily energy expenditure for primates is 3.5 times the basal metabolism (Guyton 1966), which yields daily caloric requirements for Bombacaceae-visiting mammals of 13 kcal for mouse opossums to 813 kcal for spider monkeys. An average energy requirement value of 271 kcal/day is found for 13 reported Bombacaceae-visiting mammals. To satisfy this average caloric requirement, a mammal would be required to visit and consume the entire nectar content of 35 *Ochroma* flowers. Such complete exploitation of a nectar resource is practical for the nonhovering, stationary mode of feeding of a nonflying mammal. In contrast, a hovering bat can only exploit nectar in aliquots equal to one mouthful at a time (Howell and Hartl 1980). In some Bombacaceae taxa (e.g.,

*Ceiba*) pollinating bats may alight and move among flowers much like a nonflying mammal, thus allowing more complete exploitation of available nectar (H. G. Baker, pers. comm.).

It seems unlikely that the extreme energy content of Bombacaceae flowers is a relictual feature adapted to the energy requirements of archaic, nonflying mammal visitors. The fossil remains of early marsupial and prosimian inhabitants of the neotropics suggest that they were generally smaller than contemporary mammalian inhabitants (Sussman and Raven 1978) and therefore required significantly less energy.

*Nectar-sugar composition.*—Baker and Baker (1983) have demonstrated that nectar-sugar composition is a sensitive indicator of pollinator taste preferences and have divided nectars into four classes based upon the relative amounts of sucrose and hexoses, as expressed by the S/(F + G) ratio. Among five Bombacaceae species examined quantitatively, the S/(F + G) ratio values range from 0 to 0.350 (see Table 2), indicating hexose-rich nectar. Values for this parameter of 0.904 and 0.088 were reported by Guerrant and Fiedler (1981) for *Bombacopsis quinata* (Jacq.) Dugand and *Quararibea asterolepis* Pittier, respectively. Similar qualitative results are reported herein for paper chromatographic analysis of three additional species. Those species of Bombacaceae which have been examined produce hexose-dominated or hexose-rich nectars. Hexose-dominated or hexose-rich nectar is characteristic of bat-visited flowers (especially in the neotropics) (Baker and Baker 1983), whereas the very limited data available (eight taxa) suggest that nonvolant mammal flower visitors prefer a sucrose-rich nectar (Cowling and Mitchell 1981; Baker and Baker 1983). Nectar-sugar composition of Bombacaceae is consistent with visitation by bats, but probably also could accommodate nonvolant mammal visitors.

*Nectar odor.*—As noted in Table 2, the nectars of Bombacaceae exhibit (to human olfaction) a range of fragrances from sweetly fruity to rankly aminoid. Such odors are typical of mammal-visited flowers (Sussman and Raven 1978), presumably because largely nocturnal visitors are attracted primarily by olfactory, rather than visual, stimuli. The only chemical studies of volatile constituents of Bombacaceae is that by Baldry, Dougan, and Howard (1972) in which esters, thiols, and thioesters were found to be the flavoring constituents of durian (*Durio zibethinus*) fruit. The chemical nature of volatile constituents of Bombacaceae nectars (and mammal-ingested nectars in general) remains a fruitful area for future research.

*Nectar fluorescence.*—Fluorescence of plant nectars has been noted previously (Thorp, Briggs, Estes, and Erickson 1975). During the course of the present study, it was noted that when the copious nectar of *Bombax malabaricum* was collected by pipetting, it exhibited a bluish coloration, even in full sunlight. This observation prompted an examination of the nectar under UV illumination in the dark, which revealed an intense, bright blue fluorescence. An examination of the nectars from the additional species listed in Table 2 showed that fluorescent nectar is not a general property of Bombacaceae. All nectars examined were nonfluorescent, with the exceptions of a very weak, blue fluorescence in the nectar of *Pseudobombax ellipticum* (which was not studied further) and the intense fluorescence noted above in *Bombax malabaricum.*

Paper chromatography of *Bombax malabaricum* nectar revealed a single flu-

orescent compound which was purified by paper chromatography and characterized chromatographically and spectroscopically. The fluorescent compound was shown to be the coumarin, aesculetin. The chromatographic properties of the fluorescent compound in BAW, 15% HOAc, and water and its UV spectroscopic properties were identical in all respects with those reported for aesculetin (Harborne 1960; Brackenridge 1967).

*Amino acids.*—An important nutritional factor in the diets of nectar-feeding bats is a source of dietary nitrogen. Howell and Hodgkin (1976) have suggested that intentionally (via grooming) or inadvertently ingested plant pollen is the primary nitrogen source for these bats. Field-collected nectar from members of Bombacaceae from which pollen has intentionally not been excluded contains biologically significant amounts of amino acids (see Table 2). I propose that a significant portion of the amino acids present in these nectar samples is leachate from pollen grains. Two observations support this hypothesis. Firstly, the amino acid concentration in nectar is correlated with the number of contaminating pollen grains per ml of nectar ($r = 0.95$). Secondly, species with little or no pollen contamination exhibit low, endogenously produced amino acid amounts in nectar (cf. *Pachira* in Table 2). These supporting arguments must, however, be qualified. The extreme values for number of pollen grains and amino acid concentration in *Bombax malabaricum* impart unjustified leverage to that data point in a statistical analysis. If *B. malabaricum* data are omitted, the correlation coefficient value drops to 0.21. Data from additional taxa which bridge the data gap between the clustered taxa and *B. malabaricum* will be required to confirm this postulate. In addition, the concentration of endogenously produced amino acids in nectar may vary considerably among taxa, as shown by a comparison of values for *Pachira aquatica* and *Pseudobombax grandiflorum,* neither of which contained contaminating pollen in their nectar.

The slope of the regression line (representing data from all taxa) of nectar-amino acid concentration versus pollen grains per ml of nectar yields a value of 0.047 nanomoles of amino acid which leaches out of an average pollen grain. The y-intercept value of the regression line is 0.22 m*M*. This is the statistically average nectar-amino acid concentration in the absence of contaminating pollen (i.e., the endogenously produced, amino acid concentration) and this value is consistent with that of 0.30 m*M* reported by Baker (1977) for bat-pollinated plant nectars. Amino acid concentrations of 0.390 m*M* and 12.5 m*M* were reported for nectars of *Bombacopsis quinata* and *Quararibea asterolepsis,* respectively (Guerrant and Fiedler 1981).

It is well established that amino acids leach rapidly out of pollen which is immersed in water (or nectar) (Linskens and Schrauwen 1969). These amino acids are then available to nectar-feeding visitors. Janson et al. (1981) suggested a morphological syndrome associated with nonflying-mammal flower visitors which consists of a shallow cup formed from fused perianth parts, long exserted stamens, and an upright floral orientation. I would suggest that this floral morphological adaptation serves to facilitate the presentation of a copious nectar, rich in amino acids. This syndrome allows not only accumulation of copious nectar in the base of the cup, but also facilitates the accumulation of large amounts of pollen falling by gravity from dehiscent anthers immediately above. Such a morphological pattern can be seen in such genera of bat-pollinated plants as *Bombax, Agave,*

*Ceiba,* various columnar cacti, *Cheirostemon, Ochroma.* Exceptions to this adaptive syndrome occur, notably among bat-pollinated members of the Bignoniaceae (e.g., *Kigelia*) and Leguminoseae (e.g., *Parkia*), but it seems to occur in other phylogenetically separated families as a device for presentation of a high nitrogen-content nectar.

*The existence of a nonflying-mammal phytochemical syndrome.*—There is no discernible syndrome of phytochemical floral features among examined Bombacaceae which can be associated with nonflying mammals and which is distinguishable from a bat-pollination syndrome. However, both nonflying mammals and bats are regular flower visitors of Bombacaceae and the lack of separate, distinct syndromes may reflect an adaptive compromise on the part of the plants to successfully attract both visitor types. The fact that floral caloric contents favor large-mammal needs, whereas the nectar-sugar compositions favor apparent bat-taste preferences, might be taken to support that hypothesis. In other plant groups (e.g., South African Proteaceae) in which both bats and other mammals are not concurrent pollinators, a nonflying-mammal syndrome might be more readily detectable.

Alternatively, nonflying-mammal and bat syndromes may not be resolvable. The similarities in nutritional requirements, energetic requirements, dietary diversity, and sensory systems between these two mammal groups may be so great that no nectar-offering differences are required to attract and satisfy either or both.

The detection of the remnants of any archaic phytochemical pollination syndromes (such as for archaic, nonflying-mammal pollinators of neotropical plants) is very unlikely. This is because phytochemical features (such as pigments and nectar constituents) can apparently be rapidly tailored to particular pollinator classes. The diversity of floral pigments and nectar offerings within single families such as Cactaceae (Scogin 1985) and Bignoniaceae (Scogin 1980*b*) and their tailoring to specific pollinator classes attests to the relative rapidity (in evolutionary time) with which these features can be modified. While the physiological mechanisms controlling and regulating floral pigmentation and nectar properties remain poorly understood, they have the potential for change and accommodation to the needs of specialized pollinators. The nature of these physiological mechanisms may place an upper limit on the rate of adaptive change, at least with respect to pollinator specialization and attendant phenomena of speciation and features of reproductive biology. The elucidation of these physiological mechanisms should be a major next step in our understanding of plant reproductive biology.

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## LITERATURE CITED

Altman, P. L., and D. S. Dittmer. 1972. Biology data book. Fed. of Amer. Soc. Expt. Biol., Bethesda, Md. 2123 p.

Baker, H. G. 1970. Two cases of bat pollination in Central America. Rev. Biol. Trop. 17:187–197.

———. 1977. Non-sugar chemical constituents of nectar. Apidologie 8:349–356.

———, and I. Baker. 1983. Floral nectar sugar constituents in relation to pollinator type, pp. 117–141. *In* C. E. Jones and R. J. Little [eds.], Handbook of experimental pollination biology. Van Nostrand Reinhold, New York.

Baldry, J., J. Dougan, and G. E. Howard. 1972. Volatile flavoring constituents of durian. Phytochemistry 11:2081–2084.

Brackenridge, M. I. 1967. The ultraviolet spectral analysis of coumarins. Master's Thesis. Univ. of Texas at Austin. 48 p.

Croat, T. B. 1978. Flora of Barro Colorado Island. Stanford Univ. Press, Stanford, Calif. 943 p.

Cowling, R. M., and D. T. Mitchell. 1981. Sugar composition, total nitrogen, and accumulation of C-14 assimilates in floral nectaries of *Protea* species. J. S. African Bot. 47:743–750.

Freeman, C. E., W. H. Reid, J. E. Becvar, and R. Scogin. 1984. Similarity and apparent convergence in the nectar-sugar composition of some hummingbird-pollinated flowers. Bot. Gaz. (Crawfordsville) 145:132–135.

Guerrant, E. O., and P. L. Fiedler. 1981. Flower defenses against nectar-pilferage by ants. Biotropica 13(S):25–33.

Guyton, A. C. 1966. Textbook of medical physiology. W. B. Saunders Co., Philadelphia. 1210 p.

Harborne, J. B. 1960. Plant polyphenols. 2. The coumarins of *Solanum pinnatisectum.* Biochem. J. 74:270–273.

———. 1967. Comparative biochemistry of the flavonoids. Academic Press, New York. 383 p.

———. 1977. Flavonoids and the evolution of angiosperms. Biochem. Syst. Ecol. 5:7–22.

Heithaus, E. R., T. H. Fleming, and P. A. Opler. 1975. Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. Ecology 56:841–854.

Howell, D. J. 1979. Flock foraging in nectar-feeding bats: advantages to the bats and to the host plants. Amer. Nat. 114:23–49.

———, and N. Hodgkin. 1976. Feeding adaptations in the hairs of nectar-feeding bats. J. Morph. 148:329–336.

———, and D. L. Hartl. 1980. Optimum foraging in glossophagine bats: when to give up. Amer. Nat. 115:696–704.

Hutchinson, J. 1967. The genera of flowering plants. Oxford Univ. Press, London. 659 p.

Janson, C. H., J. Terborgh, and L. H. Emmons. 1981. Non-flying mammals as pollinating agents in the Amazonian forest. Biotropica 13(S):1–6.

Linskens, H. F., and J. Schrauwen. 1969. The release of free amino acids from germinating pollen. Acta Bot. Neer. 18:605–614.

Niranjan, G. S., and P. C. Gupta. 1973. Anthocyanins from the flowers of *Bombax malabaricum.* Planta Med. 24:196–199.

Nowak, R. M., and J. L. Paradiso. 1983. Walker's mammals of the world. Johns Hopkins Univ. Press, Baltimore, Md. 1362 p.

Pomilio, A. B., and J. F. Sproviero. 1973. Anthocyanins from flowers of *Hibiscus cisplatinus* and *Chorisia speciosa.* Anales Asoc. Quim. Argent. 61:45–46.

Porsch, O. 1935. Säugetiere als Blumenausbeuter und die Frage der Säugetierblume. II. Biol. Gen. 11:171–188.

Pyke, G. H. 1980. The foraging behavior of Australian honeyeaters: a review and some comparisons with hummingbirds. Austral. J. Ecol. 5:343–369.

———, and N. Waser. 1981. The production of dilute nectars by hummingbirds and honeyeater flowers. Biotropica 13:260–270.

Robyns, A. 1964. Flora of Panama-Bombacaceae. Ann. Missouri Bot. Gard. 51:37–68.

Scogin, R. 1979. Anthocyanins of the Sterculiaceae. Biochem. Syst. Ecol. 7:35–36.

———. 1980*a*. Floral pigments and nectar constituents of two bat-pollinated plants: coloration, nutritional, and energetic considerations. Biotropica 12:273–276.

———. 1980*b*. Anthocyanins of the Bignoniaceae. Biochem. Syst. Ecol. 8:273–276.

———. 1985. Nectar constituents of the Cactaceae. Southw. Nat. 30:77–82.

Steiner, K. E. 1981. Nectarivory and potential pollination by a neotropical marsupial. Ann. Missouri Bot. Gard. 68:505–513.

Start, A. N., and A. G. Marshall. 1976. Nectarivorous bats as pollinators of trees in West Malaysia, pp. 141–150. *In* J. Burley and B. T. Styles [eds.], Tropical trees: variation, breeding, and conservation. Academic Press, New York.

Sussman, R. W., and P. H. Raven. 1978. Pollination by lemurs and marsupials: an archaic coevolutionary system. Science 200:731–736.

Thorp, R. W., D. L. Briggs, J. R. Estes, and E. H. Erickson. 1975. Nectar fluorescence under ultraviolet irradiation. Science 189:476–478.

Timberlake, C. F., and P. Bridle. 1975. The anthocyanins, pp. 214–266. *In* J. B. Harborne, T. J. Mabry, and H. Mabry [eds.], The flavonoids. Academic Press, New York.

Toledo, V. M. 1977. Pollination of some rain forest plants by non-hovering birds in Veracruz, Mexico. Biotropica 9:262–267.

Yemm, E. W., and E. C. Cocking. 1955. The determination of amino acids with ninhydrin. Analyst 80:209–213.